Variation of scavenger richness and abundance between sites of high and low iceberg scour frequency in Ryder Bay, West Antarctic Peninsula

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Abstract

Physical disturbance, particularly from iceberg scour, is a major structuring force in polar benthic communities at shelf depths. Scouring kills and damages benthic organisms providing food for the abundant scavenging fauna of coastal Antarctic waters. This trophic group is likely to be strongly affected by changes in iceberg scouring. A baited underwater camera system was used to examine the distribution of scavenging fauna in relation to the spatial variation in exposure to iceberg impacts experienced at different iceberg scouring conditions and depths within Ryder Bay. The results indicate that the relationships between depth and scavenger abundance and assemblage composition differed between high and low scour sites. Scavenger abundance increased with depth at high scour sites and fell with depth a low scour sites. There was also significant difference in community composition between sites within each scouring condition. Scavenger species richness also exhibited an increase with depth at most sites consistent with the established pattern of declining iceberg scouring frequency with depth. Shannon Wiener Diversity increased with depth but significantly more steeply in highly-scoured sites. Our results suggest that depth and exposure to icebergs interact to shape the scavenger community. The significant differences within the high and low scour groups suggest that other factors remain to be investigated and that there is probably a non-linear relationship between scouring intensity and the favourability of a site for scavengers.

Key Words

Scavengers. Western Antarctic Peninsula. Iceberg scouring. Baited underwater camera. Patterns of distribution.

Introduction

Physical disturbance, particularly from iceberg scour, is a major structuring force in polar benthic communities at shelf depths (Bergeron and Bourget 1986; Teixido et al. 2004; Barnes and Conlan 2007). Sea ice and anchor ice, "submerged ice attached or anchored to the bottom", also disturb the seafloor around Antarctica (Gutt 2001). When icebergs collide with the sea bed in shallow coastal waters (<50 m) (Pearse et al. 1991; Dowdeswell et al. 1993; Peck et al. 1999; Brown et al. 2004) they can plough and displace soft marine sediments or abrade rocky substrata (Pugh and Davenport 1997) and are one of the

most destructive natural forces affecting benthic environments at depths of < 400 m (Gutt 2001; Smale et al. 2007b). The Antarctic continental shelf break is unusually deep, on average 450 m (but up to 1000 m), compared to shelves elsewhere (100 - 200 m), from depression by continental ice sheets, scouring by grounding ice shelves during glaciations (Clarke and Johnston 2003) and a lack of riverine deposition of sediment, common in the Arctic (Rachold et al. 2004). Gutt (2000) and Gerdes et al. (2003) found that an estimated 5 % of the Antarctic shelf seafloor (< 500 m) was affected by iceberg scouring over a 14 year period. Studies of the growth rates of the bivalve mollusc *Yoldia eightsi* indicated that areas at 9 m in a single cove on Signy Island were scoured every 50 - 75 years (Peck and Bullough 1993; Peck et al. 1999). Grounding frequencies increase with decreasing depth primarily due to there being many small icebergs from sea ice and few 100 km scale tabular icebergs (Gutt et al. 1996; Barnes 1999; Smale et al. 2007a; Smale et al. 2007b). Keel depth restricts the movement of larger icebergs to deeper parts of the continental shelf (Hequette et al. 1999) and impacts by these larger icebergs are infrequent but of a high intensity due to their greater mass and momentum (Smale et al. 2008).

Iceberg scouring causes a significant reduction in benthic biomass and biodiversity on a small spatial scale (Conlan and Kvitek 2005). Reductions of up to 99.5 % of mega and macrobenthos within the area of impact have been measured (Peck et al. 1999; Smale et al. 2007b). Distinct differences in benthic assemblages are apparent between newly impacted and non-impacted sites leading to a mosaic of nearshore benthic communities at different stages of recovery (Barnes and Conlan 2007; Barnes and Conlan 2012). This promotes between habitat biodiversity (β- diversity) (Gutt et al. 1996; Gerdes et al. 2003; Gutt and Piepenburg 2003), variability of habitat and biological assemblages at both spatial and temporal scales and regional polar benthic richness (Peck et al. 1999; Smale et al. 2007b; Smale et al. 2008).

Clear changes in Antarctic benthic assemblages with depth in the sublittoral environment have been observed by several studies (Barnes 1995; Bowden 2005; Smale 2008) and suggested to be largely due to the recognised pattern of decreasing iceberg scouring frequency with depth (Barnes 1995; Barnes 1999). Shallow areas of heavily disturbed sites are characterised by assemblages of low diversity and biomass able to rapidly re-colonise following impacts (Peck et al. 1999; Gutt and Piepenburg 2003; Teixido et al. 2004; Smale et al. 2007a). Intermediate frequencies of ice disturbance are thought to enhance diversity by preventing species domination and creating a patchwork of habitat and communities in various stages of recovery (Brown et al. 2004; Conlan and Kvitek 2005; Smale et al. 2007a). Such communities, representative of intermediate levels of disturbance, were found in areas where ice scouring occurred every 10 years in the High Canadian Arctic (Conlan and Kvitek 2005) and between 5 and 50 m in Antarctica (Peck et al. 1999).

Recent scours are dominated by opportunistic scavengers attracted to feed upon the carrion produced by the impact (Gutt 2001). Mobile scavengers dominated the early recolonisation (by megabenthos) of new scours at Anvers Island (Richardson and Hedgepeth 1977), McMurdo Sound (Lenihan and Oliver 1995), Signy Island (Peck et al. 1999), Adelaide Island (Smale et al. 2007b; Smale et al. 2007c) and in the Southeastern Weddell Sea (Gerdes et al. 2003). Scavengers provide an essential ecosystem service by recycling the nutrients and energy enclosed in carrion (Priede et al. 1990; Bailey et al. 2007) and thus probably play a major role in the nearshore environment of much of coastal Antarctica where they are prevalent in the megafauna (Brown et al. 2004; Smale et al. 2007c). Scavenging is a strategy employed by many mega and macro benthic organisms in Antarctica and many have omnivorous diets, which allows them to utilise the

carrion produced by scouring impacts (Dayton et al. 1994; Smale et al. 2007c; Gillies et al. 2012). Despite the potential importance of ice scouring impact to the dynamics of this dominant group in the Antarctic megafauna there has been limited study of scavenger abundance and behaviour in relation to spatial and temporal differences in scouring impact. Previously a single study was carried out to examine the colonisation process of scours by scavengers in two heavily ice impacted environments in Ryder Bay, Adelaide Island, Western Antarctic Peninsula (WAP), using an artificial bait representing the carrion from a scouring event (Smale et al. 2007c). Megafaunal aggregations were dominated by the brittle star *Ophionotus victoriae*, the omnivorous asteroid *Odontaster validus*, the scavenging/predatory nemertean *Parborlasia corrugatus*, the lysianassid amphipod *Cheirimedon femoratus* and the echinoid *Sterechinus neumayeri* (Smale et al. 2007c). The species composition of the scavengers observed in this study contrasted significantly between the two study sites, only 1 km apart. Smale et al. (2007c) suggested that the differences in scavenger composition were linked to the differences in substratum type and exposure to scouring between the sites. Iceberg scouring is predicted to change under conditions of climate change however, the relationships between scouring intensity and scavenger assemblage composition are unknown. It is important to improve our understanding of the scavenging fauna's response to iceberg scouring intensity in order to predict how Antarctic benthic community structure and function might vary under future scenarios where the supply and mobility of icebergs is different.

The objective of this study was to investigate how scavenger distribution and abundance varied between three depths and at high and low iceberg scouring conditions experienced at four sites in Ryder Bay, Adelaide Island. This expands on the study by Smale et al. (2007c) by including two more sites observed to experience lower scouring impact and three depths thus allowing a study of scavenger assemblage composition over a greater range of scouring intensities and frequencies. This study represents the first examination of how Antarctic benthic scavenger richness and relative abundance varies in relation to the recognised pattern of decreasing iceberg scouring frequency and impact with depth. Data for this investigation was gathered using a novel baited underwater camera (BUC) system. Greater scouring generates more carrion and thus favours scavenging strategies leading to our first hypothesis that scavenger richness and abundance would be highest at high scouring conditions and sites. Our second hypothesis is that scavenger richness and abundance would peak at depths where intermediate levels of scouring impact were experienced and that the depth of peaks would be expected to be shallower under low scouring impact conditions.

Materials and methods

Study area

BUC deployments were made at two sites: Hangar Cove (HC) and South Cove (SC), adjacent to the British Antarctic Survey (BAS) Rothera Research Station (67°34′07″S, 68°07′30″W), Adelaide Island and at two sites in Ryder Bay: Rose Garden (RG) (67°36′76″S, 68°12′70″W) and Trolval Island (TI) (67°35′70″S, 68°12′50″W) (Fig. 1). The area of each site was approximately 0.5 km^2. Both HC and SC have a similar bathymetric profile (ca. 30˚) (Smale et al. 2007a; Brown et al. 2004) but different substratum. HC has compacted cobbles overlaid with silt, while SC has a mixture of bedrock and compacted cobbles (Smale et al. 2007a; Smale et al. 2007c). HC is exposed to the prevailing winds, which bring large numbers of icebergs in during the Summer (Smale et al. 2007c). SC is less exposed to winds but icebergs are frequently

transported in by currents leading both sites to be described as highly scoured by previous studies (Smale et al. 2007a). HC and SC were selected as data on iceberg scouring frequency and intensity have been collected at those sites for over a decade (Brown et al. 2004; Barnes and Souster 2011).

The substratum at TI is bedrock, overlaid with sediment and dominated by macro-algae, and RG consists of bedrock with occasional loose boulders and patchy macro-algae. RG and TI were chosen as sites considered to experience low scour conditions due to regular observations of the rate of iceberg grounding by BAS scientists and the dense covering of macro-algae, only able to survive under low scouring regimes. The topography present also prevents most icebergs reaching these sites (D. Barnes pers obs).

BUC deployments within HC and SC were classified as being in high scour impact conditions and those in RG and TI in low scour conditions. Within each of the four sites (HC, RG, SC and TI) the locations for three stations were the first three positions from a list of randomly generated coordinates within the designated study area. At each station a deployment was made at 5, 10 and 25 m depth in a line perpendicular to the contour. Three replicate deployments were made per depth per site and a total of 36 deployments across the four sites. Deployments timing were chosen using a rotational matrix, which ensured that two deployments were not made consecutively in the same site. This was to allow bait plumes to disperse and to give an opportunity for scavengers to resume their previous behaviours and distributions. The use of the matrix also ensured that all deployments at a particular site or depth were not made at the same time of day. Deployment details are in Table. 1.

A SeaLife DC 1000 underwater camera, on an L-shaped aluminium frame, recorded digital stills of the bait at 1 frame every 30 s and was illuminated by two Epoque ES-23DS strobes. A Nortek Aquadopp acoustic Doppler current meter (Aquadopp Current Meter, Nortek, USA) was attached to the vertical element of the frame to record depth, current direction and speed. The frame was held upright in the water column by a sub-surface buoy and was deployed and recovered using a mooring line and surface buoy (Fig. 2) for a minimum of 90 minutes. The camera field of view covered an approximate 2 m^2 area of the seabed however, this would vary slightly with the topography. A bait was suspended, just off the seabed, in the middle of the bottom of the camera field of view and had a total mass of 200 g (50 g each of freshly chopped *O. victoriae*, *O. validus*, *S. neumayeri* and *Laternula elliptica*) contained within a mesh bag. This bait was intended to be representative of the local benthic fauna and therefore of the food types made available through iceberg scouring. The increased attraction of scavengers to the BUV, compared to unbaited deployments, makes it less likely to produce low or zero abundance estimates allowing for more statistical powerful relative comparisons in scavenger relative richness and abundances (Wills and Babcock 2000; Stoner et al. 2008). Images of scavengers generated by the BUC system are displayed in Fig. 3.

180 images were recorded in each deployment and the resolution and lighting was altered using batch processed in Adobe Photoshop CS5 to facilitate species identification. The total number of individuals of each scavenger species was recorded in each image. A scavenger is defined as organisms "able to detect carrion, usually by either distance or touch, chemoreception, or both, deliberately to move towards it, and eventually consume either part or all of it" (Britton and Morton 1994).

Data analysis

Data on the species and abundance of scavengers observed in the BUC was analysed across the four sites, two iceberg scouring impact conditions (high and low) and across the three depths 5, 10 and 25 m. The following statistical tests tested hypothesis one, that scavenger richness and abundance would be significantly different between high and low impact sites, and two, that scavenger richness and abundance would vary significantly with depth.

Species observed in the BUC were categorised into taxonomic groupings (Table. 2), some containing a single species, e.g. *S. neumayeri* was the only Echinoidea. For each deployment the relative abundance metric; the maximum number of individuals observed in one image in the camera (Max_N) was recorded for each scavenger species. Max_N avoids repeated counts of the same individual and provides a conservative estimate of the relative abundance since only a proportion of the scavengers in the area will be observed in the camera at once (Harvey et al. 2012). Differences in the scavenger assemblages between iceberg impact condition, depths and sites were compared using differences in the Max_N of scavengers. Initially replicated data of Max_N was log (x +1) transformed to down-weight the importance of the highly abundant echinoderm *S. neumayeri*. Three trial deployments were made in SC to determine the time required for the Max_N to be reached. Trial deployments lasted three hours and the Max_N of each of the scavenger groups was reached within 90 mins (Fig. 4). The number of scavenger species observed at the BUC over the whole deployment was used as a measure of species richness and the Shannon-Wiener diversity index was derived from a matrix using Max_N as an index of abundance. Data on species richness, relative abundance, as measured by the index Max_N, and the Shannon-Wiener diversity index were averaged (± SE) across the three replicate deployments for each site.

The response variable Max_N for the four most common scavenger species *O. validus*, *O. victoriae*, *P. corrugatus* and *S. neumayeri* and the predictors high and low impact condition, depth, site (nested with impact condition), mean current speed and their interactions were modelled using a Generalized Linear Model (GLM) using the R package MASS. GLMs are particularly useful for modelling count data. Count data can often have a variance greater than the mean, known as overdispersion. If overdispersion was detected a GLM with a negative binomial distribution was used (GLM NB), which represent models appropriate for the modelling of overdispersed data.

Differences in Max_N assemblage were examined using a three factor design non-parametric multivariate analysis in PERMANOVA (Anderson 2001; Anderson et al. 2008) with scouring impact condition (fixed factor, two levels), site (random factor, nested with impact condition) and depth (fixed, three levels). Differences in assemblage composition were visualised in non-metric multi dimensional scaling (nMDS) plots. A SIMPER analysis examined the role of individual species in the average Bray-Curtis dissimilarity based on Max_N as an index of relative abundance.

Results

The mean species richness of scavengers increased significantly with depth at all sites in BUC deployments (GLM NB, $p < 0.05$). When individual sites were examined mean (± SE) species richness increased between 5 and 25 m at RG (from 2 species ± 0 deployment^{-1} to 3.33 ± 0.19) and at SC (2 species ± 0.33 to 5.33 ± 0.19) and peaked at 25 m at TI (4 species ± 0.33) and at 10 m in HC (3.67 species ± 0.19) (Fig. 5a). The Shannon-Wiener diversity index increased significantly with depth in deployments in all sites but in both

high scour sites the incline was steeper due to both having lower indexes at 5 m (GLM, $p < 0.05$) (Fig. 5b). The mean Max_N of all scavenger species was significantly different between sites (GLM NB, $p < 0.005$) and scouring impact condition (GLM NB, $p < 0.005$). The mean Max_N also varied significantly with depth (GLM NB, $p < 0.05$) and a significant interaction factors showed that the relationship between mean Max_N and depth is dependent on both the site and impact condition (GLM NB, $p < 0.001$ and $p < 0.001$). In high impact conditions at SC mean Max_N (± SE) increased between 5 and 25 m (from 16.67 individuals ± 2.69 deployment^{-1} to 66 ± 8.08) and at HC mean Max_N was higher at both 10 and 25 m (63.33 individuals ± 15.03 and 35.67 ± 7.40) than at 5 m (32 individuals ± 6.66). Under low impact conditions at TI mean Max_N declined between 5 and 25 m, (from 84 individuals ± 16.09 to 36.33 ± 7.18). At RG mean Max_N was lower at both 10 and 25 m (13.67 individuals ± 1.64 and 24.33 ± 1.39) compared to 5 m (39.33 ± 8.38) (Fig. 5c). GLM results and models are in Table 3.

Notothenia coriiceps, *Harpagifer antarcticus*, *Glyptonotus antarcticus* and *Flabelligera mundata* were rarely seen and often only observed at a single site (Table. 2) therefore, further analysis concentrated on the four most common species: *O. validus*, *O. victoriae*, *P. corrugatus* and *S. neumayeri*. On examination of individual scavenger species using the GLM analysis the Max_N of *O. validus* was significantly different between sites (GLM NB, $p < 0.05$). *O. validus* distribution between sites was coincident with their impact condition (GLM NB, $p < 0.05$) and higher relative abundances of *O. validus* were observed in low impact condition sites. *O. validus* Max_N also generally increased with depth (GLM NB, $p < 0.05$) in deployments at all sites but at each depth Max_N was significantly higher in low impact deployments (Fig. 6a). The Max_N of *O. victoriae* varied significantly with depth in deployments under both impact conditions (GLM NB, $p < 0.001$). *O. victoriae* was only observed at 25 m in deployments at TI and primarily at 25 m in deployments at HC and SC (Fig. 6b). The Max_N of *P. corrugatus* varied significantly between sites and impact conditions (GLM NB, $p < 0.05$ and $p < 0.05$) and with depth (GLM, $p < 0.05$). A significant interaction between impact condition and depth was observed (GLM, $p < 0.05$). The Max_N of *P. corrugatus* peaked at 10 m in HC and SC. *P. corrugatus* was however, rare at RG (2 in 9 deployments) and high at TI (27 individuals deployment^{-1} ± SE 3.7). Only at TI did *P. corrugatus* Max_N decline from 5 m (49 individuals ± 13.05) to 25 m (1 ± 0.58) (Fig 6c). The Max_N of *S. neumayeri* varied significantly between impact condition and sites (GLM NB, $p < 0.05$ and $p < 0.05$). The Max_N of *S. neumayeri* decreased significantly with depth in deployments in both high and low iceberg impacts conditions (GLM NB, $p < 0.005$). A significant interaction factor was observed between condition and site and *S. neumayeri* Max_N only declined between 10 and 25 m in high scour conditions due to the low Max_N observed at 5 m (Fig. 6d).

Bray-Curtis similarity nMDS plots (Fig. 7) and PERMANOVA analysis (Table 4) distinguished between scavenger assemblages in deployments at the four sites and three depths. Using the Max_N of the observed scavengers, assemblages varied significantly between deployments in the four sites ($p < 0.005$). Assemblage pattern also varied significantly with depth ($p < 0.001$) and a significant interaction between depth and impact condition was observed ($p < 0.05$). Pairwise comparisons revealed that the greatest dissimilarities in scavenger assemblages were between 5 and 25 m and the lowest between 5 and 10 m. The difference between the Max_N of scavenger assemblages varied most between RG and all other sites. This was primarily due to the unique asteroid rich assemblages at RG (*O. validus* and *Cryptasterias turqueti*), which was in contrast to the other three sites where scavenger assemblages were dominated by larger numbers of *O. victoriae*, *P. corrugatus* and *S. neumayeri*. The scavenger assemblage was significantly different between HC and TI and SIMPER analysis revealed that this was mainly due to the larger number of asteroids (*C.*

turqueti and *O. validus*), *P. corrugatus* and *O. victoriae* that arrived in deployments in TI making the assemblages differ from that at HC where few of these scavengers arrived. SIMPER analysis also found that *S. neumayeri* and *O. victoriae* were primarily responsible for the differences in scavenger assemblages observed between 5 m and 25 m and between 10 m and 25 m. The assemblage differences between 5 and 10 m were primarily due to different abundances of *S. neumayeri*, *P. corrugatus* and *O. validus.*

Discussion

The scavengers that visited the BUC (particularly *O. victoriae*, *O. validus*, *S. neumayeri* and *P. corrugatus*) are common in shallow Antarctic benthic environments subject to ice disturbance (Kidawa 2001; Cranmer et al. 2003) and are known to congregate at scour carrion (Smale et al. 2007c) or bait (McClintock 1994; Thiel and Kruse 2001). The richness of scavenger assemblages was relatively similar across the four sites and *O. victoriae*, *O. validus*, *S. neumayeri* and *P. corrugatus* were common to all sites. However, the scavenger assemblages recorded by the BUC were significantly different between sites and showed differences in the relative proportions of individual species. Scavenger species richness also exhibited an increase with depth at most sites consistent with the established pattern of declining iceberg scouring frequency with depth. Results indicate that the relationships between depth and scavenger abundance and assemblage composition differed between high and low scour sites. The general pattern was that the relative abundance of scavengers increased with depth at the sites experiencing high ice scour impact and declined with depth at low impact sites. The relative ability of individual scavenger species to survive and benefit from iceberg scouring, along side other additional feeding strategies, can be used to help explain their distribution in relation to the declining frequency of iceberg scouring impact with depth.

Iceberg scouring intensity is likely to have a range of interacting effects on scavengers. As well as utilising the carrion from scouring events scavengers can also become carrion themselves and the amount of carrion produced by an event is dependent on the time between scours for benthic biomass to recover. Under very high intensity scouring conditions there will be limited benthos to kill and a high mortality of scavengers. Whereas, in very low intensity scouring conditions there will be very little carrion for scavengers to feed upon. Somewhere between very high and very low scouring frequency will be a scouring frequency that will provide the optimal trade-off between carrion and survival for scavengers however, where this falls will be dependent on the scavenger's life history.

When the relative abundances of the main scavenger species was examined using the BUC system the greater relative abundance of the asteroids at the low scoured sites was a major difference between assemblages at high and low scoured sites. The relative abundance of the most common asteroid *O. validus* was higher in both the highly scoured sites. In low impact conditions more asteroids (Nonato et al. 2000; Palma et al. 2007) were able to thrive and dominate scavenger assemblages. Asteroids have also been reported as common below 15 m at Anvers Island, WAP, where they were only infrequently disturbed by impacts with larger icebergs (Koplovitz et al. 2009). Some of the asteroid species, *C. turqueti* and *Diplasteri as brucei*, have brooding developmental strategies (Pearse et al. 1994; McClintock and Pearse 1986) and require a long development time and are only able to develop where ice disturbance is infrequent (Nonato et al. 2000; Palma et al. 2007). *O. validus* larvae however, undergo a brief pelagic period but larvae and embryos are largely demersal and require a development period of approximately 6 months to reach metamorphosis (Pearse 1969).

Both RG and TI have been observed to experience low iceberg impact but significant differences were observed between their scavenging assemblages. At RG *P. corrugatus* was rare and *O. victoriae* absent. However, RG supported rich asteroid assemblages particularly at 25 m and was the only site where species such as *Porania antarctica glabra* and *G. antarcticus* were only seen. Also differences between individual species were observed; *P. corrugatus* relative abundance was very different between the two low scour condition sites. The reasons for this are not known but might lie in the high level of spatial and temporal variability with which scouring occurs even within areas of the same overall level of iceberg scour. Small scale variation in iceberg disturbance has been found at the same site and depths in SC (Smale et al. 2007a) and studies of impact frequency and intensity using impact blocks have found that results can differ substantially between study years. Contrasting results were found between the studies by Brown et al. (2004) where HC experienced 3 times more scouring events than SC and Smale et al. (2007a) who recorded a 1.5 times greater disturbance intensity and frequency at SC compared to HC. This illustrates that as observed between HC and SC a high level of variability in recent scouring frequency could exists between the two low scoured sites. The distribution of the individual scavengers classes examined in this study would indicate that the frequency of scouring at RG is lower than TI. Possibly scouring is so low at the depths studied that *P. corrugatus* has limited carrion to feed upon and low abundances are found at this site. Richer assemblages of asteroids are able to develop at shallower depths than TI due to the reduced iceberg scouring frequency experienced at 25 m. Also other species that potentially only survive under very low iceberg impact conditions start to appear in the assemblages (e.g. *G. antarcticus*). Assigning clear levels of impact to each site is therefore problematic even when impact blocks are used, with sites varying temporally as well as spatially in their level of impact. While TI and RG have been assigned to a "low impact" group we do not have a quantitative measure of scouring intensity for these areas.

Hypothesis one must be rejected as the relative abundance of scavenger populations between high and scour conditions is more complicated than predicted due to the different life histories of individual scavenger species and potentially varying ice scour frequency between sites within each scouring condition.

Depth

A decline in iceberg scouring frequency with depth has been well documented (Gutt 2001) and was recorded at HC and SC in Ryder Bay by Smale et al. (2007a). Grounding frequencies decrease with depth primarily due to there being many small icebergs frequently impacting shallow depths (Gutt et al. 1996; Barnes 1999; Smale et al. 2007a; Smale et al. 2007b). Impacts are more infrequent at deeper depths where the keel of most icebergs cannot reach (Smale et al. 2007a). Several published studies have found that the richness of Antarctic benthic communities in shallow subtidal areas increases with depth (Smale 2008; Sahade et al. 1998; Nonato et al. 2000). Iceberg scouring has been suggested as a driving force behind the increase in assemblage richness with depth (Peck and Bullough 1993; Sahade et al. 1998). Biological factors and competition become more important at depths or areas experiencing little ice impact. The highest richness of benthic communities have been recorded where intermediate levels of scouring impact enable a range of species to survive but where the monopolisation of dominant species is prevented (Brown et al. 2004; Conlan and Kvitek 2005). This research is the first investigation of Antarctic benthic scavenger distribution with depth and demonstrates that the species richness of the scavenger assemblages increased with depth. However, the distribution of scavenger relative abundance increased with depth at the sites experiencing high ice scour impact and declined with depth at low impact sites. The increase in the relative abundance of

scavengers at high scoured sites was coincident with the decrease in scouring frequency with depth. At the shallowest depths, only a few highly mobile species, such as *S. neumayeri*, were observed, probably due to their ability to quickly re-colonise a scour and persist through broad feeding flexibility. At 5 m at the highly scoured sites a high proportion of hard surfaces were bare (of mega and larger macrofauna) due to slow recolonisation and growth of assemblages under high scour frequency (Sahade et al. 1998; Gutt 2001) which with high grazing pressures from *Nacella concinna* (Bowden et al. 2006) are held at early successional stages (Smale et al. 2007a). *S. neumayeri* have been found to be most abundant at shallow depths in previous studies (Smale et al. 2008) and to form dense grazing aggregations at shallow depths where algal densities are high. As well as utilising the carrion from scouring events scavengers can also become carrion themselves. At 5 m in 'high scoured conditions' the frequency of scouring is intense (approximately mean 3 impacts per 16 m^2 grid per month at both SC and HC) (Smale et al. 2007a). The typically short time between impacts allows little benthic biomass to develop, so following impacts there will be relatively little carrion. *P. corrugatus* has a voracious appetite (Heine et al. 1991) and its distribution is therefore likely to be linked to carrion supply. 10 m is potentially where the most effective trade off between a sufficient carrion supply and damage from iceberg scouring exists for *P. corrugatus*. *O. victoriae* was almost exclusively observed at 25 m regardless of scouring condition. A similar observation was made by Nonato et al. (2000) and Palma et al. (2007) at King George Island. *O. victoriae* is a generalist carnivore and its distribution could be affected by the presence of another food source, such as settling phytoplankton (Obermuller et al. 2010) or a physiological adaptation to deeper depths.

Contrasting patterns of relative scavenger abundance with depth were however, observed between high and low scouring conditions, and the relative abundance of scavengers declined with depth in low scoured sites, leading us to accept hypothesis two. In the low impact condition the frequency of impacts was expected to be relatively low even at the shallowest depths, declining further as depth increases. The relative abundance of *P. corrugatus* and *S. neumayeri* was generally highest at 5 m and declined with depth. At 10 and 25 m the impact of iceberg scouring is potentially very low at these sites and limited or infrequent carrion is produced for *P. corrugatus* and *S. neumayeri* to feed upon corresponding to a reduction in their relative abundance. *S. neumayeri* is also distributed in shallower depths to utilise algal colonies. *P. corrugatus* was however, almost absent at RG potentially linked to the very low level of scouring and carrion at the site. Asteroids dominated areas experiencing low iceberg scouring frequency and the relative abundance of *O. validus* (by far the most abundant seastar), increased with depth. *O. validus* is also a predator of sponges (Dayton 1989) so increases in relative abundance with depth could also be linked to the richer sponge communities observed in deployments at 25 m in RG and TI.

This study examined the distribution of scavenger assemblages during a single summer season and previous studies have demonstrated that these species and assemblages exhibit high seasonal variability in their distribution (Smale et al. 2007c; Obermuller et al. 2001). Patterns of scavenger distribution could therefore, vary during spring, winter and autumn when rates of scouring (Smale et al. 2007a) and primary production (Whitaker 1982) are very different. The present study highlights data gaps in the understanding of the migration pattern of the 'deeper' scavenger species, which were difficult to study routinely using scuba diving surveys. Within the scope of this study it was not possible to investigate the possible roles of factors such as the distribution of benthic and pelagic primary production, turbidity or wave effect. The lack of quantitative measurements of iceberg scouring intensity is a significant weakness, but something that could be incorporated into a larger study in the future.

Conclusion

This study has provided new insights into the macrobenthos scavenger richness and abundance in the shallow Antarctic environment in relation to iceberg scouring impact. Our results suggest that depth and exposure to icebergs interact to shape the scavenger community. The significant differences within the high and low scour groups suggest that other factors remain to be investigated and that there is probably a non-linear relationship between scouring intensity and the favourability of a site for scavengers.

Acknowledgements

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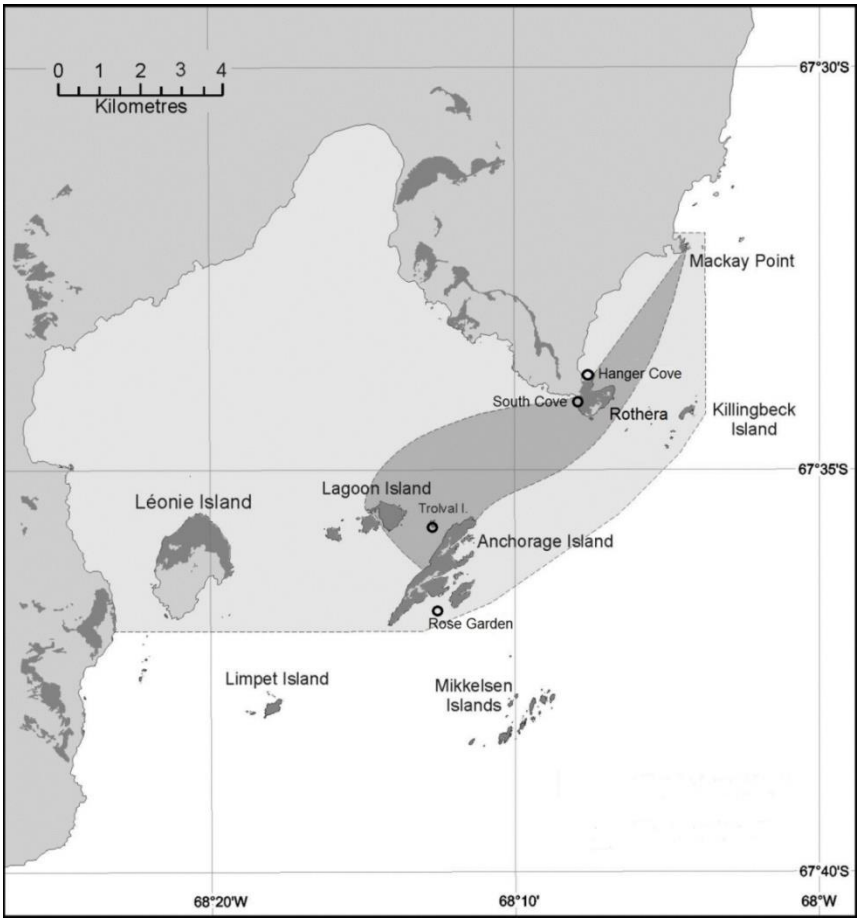
Figures and Legends

(a)



(b)

Adelaide Island

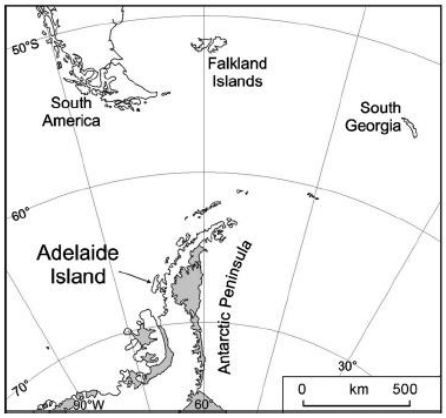


Figure 1. Location of a) Adelaide Island in relation to the Antarctic Peninsula and b) Hangar Cove (HC), Rose Garden (RG), South Cove (SC) and Trolval Island (TI) in relation to Rothera Point, Adelaide Island, Western Antarctic Peninsula. Lighter shading in the ocean describes the Ryder Bay area and the darker shading the Rothera boating limits.

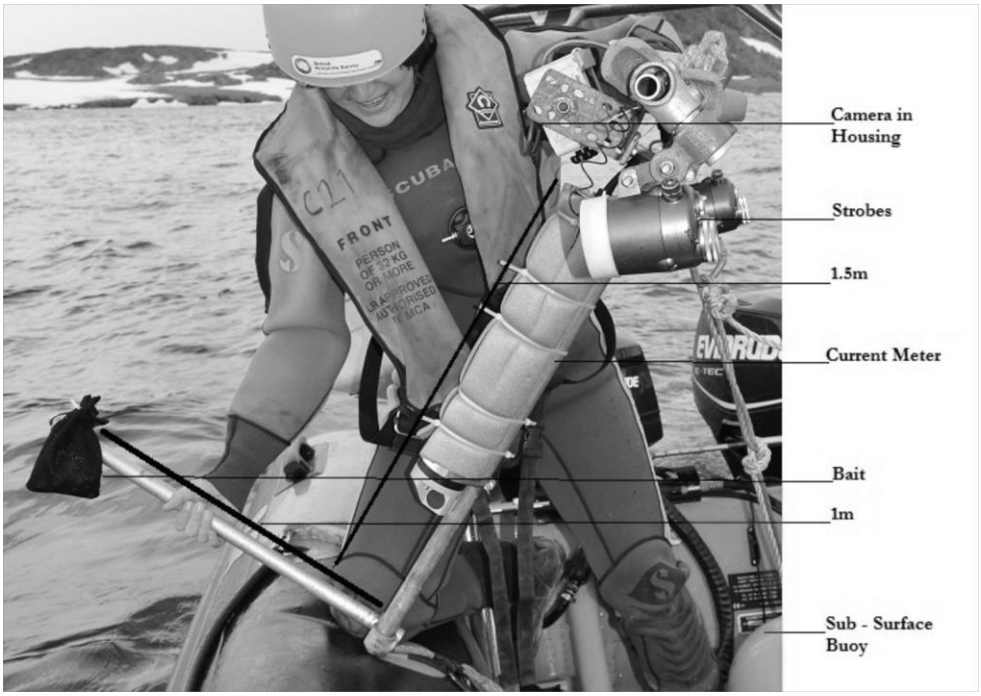
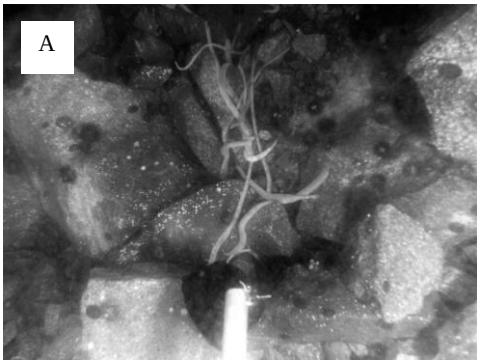


Figure 2. Baited underwater camera equipment used to record the accumulation of scavengers at Ryder Bay, Western Antarctic Peninsula.



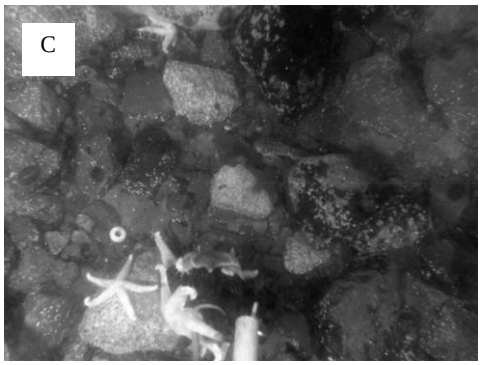


Figure 3. Plot of the arrival pattern of scavengers at a trial baited underwater camera deployment at 10 m in South Cove.

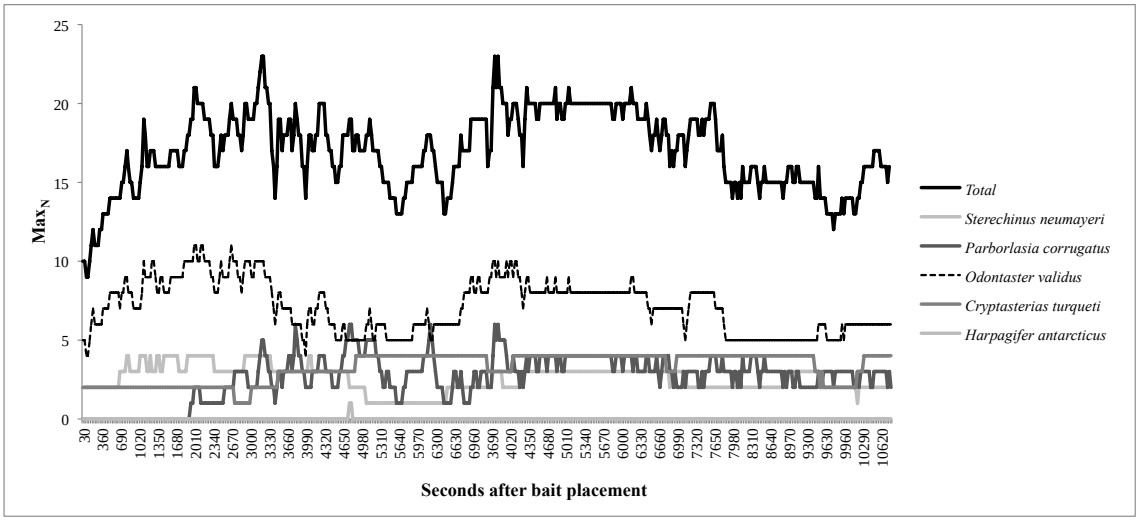


Figure 4. Images recorded by the BUC at a) 10 m at high scoured Hangar Cove containing *Sterechinus neumayeri* and *Parborlasia corrugatus*, b) 25 m at high scoured South Cove containing *Ophionotus victoriae* and asteroids and c) 10 m at low scoured Rose Garden containing *Odontaster validus*, and *Cryptasterias turqueti.*

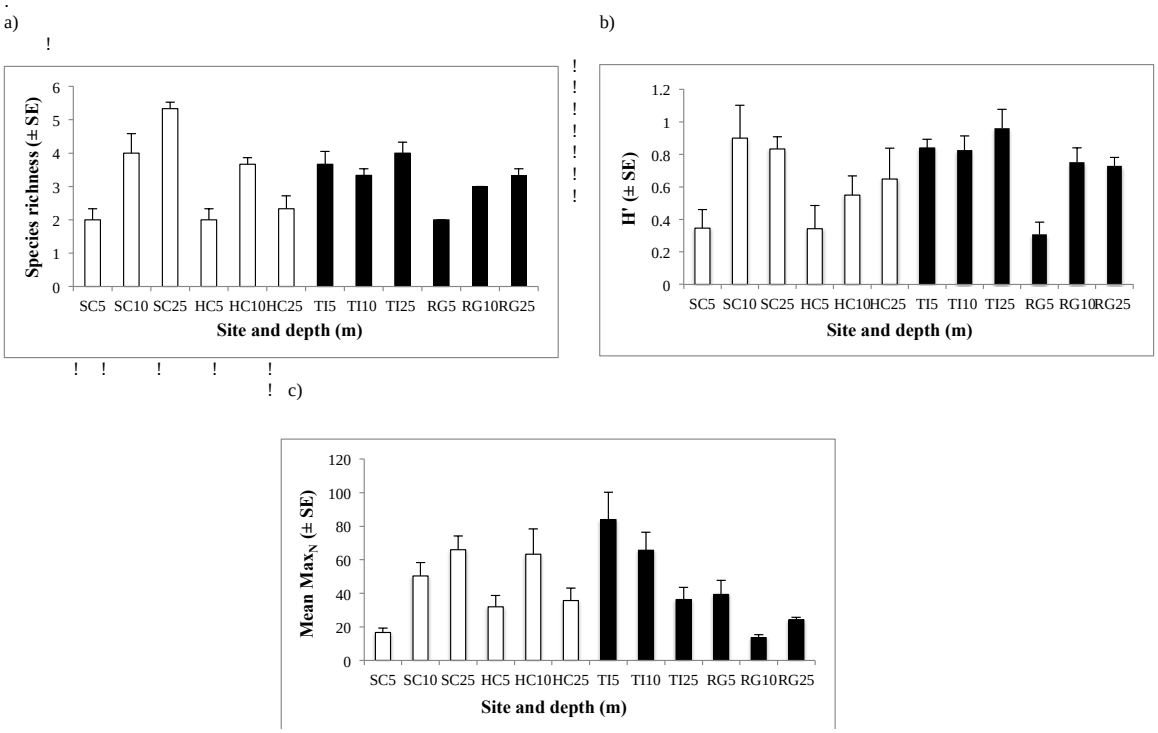


Figure 5. Mean (± SE) species richness recorded in BUC deployments at the four sites; South Cove (SC), Hangar Cove (HC), Rose Garden (RG) and Trolval Island (TI) and at three depths; 5, 10 and 25 m. Low iceberg scouring impact site represented by open bars and high by closed bars.

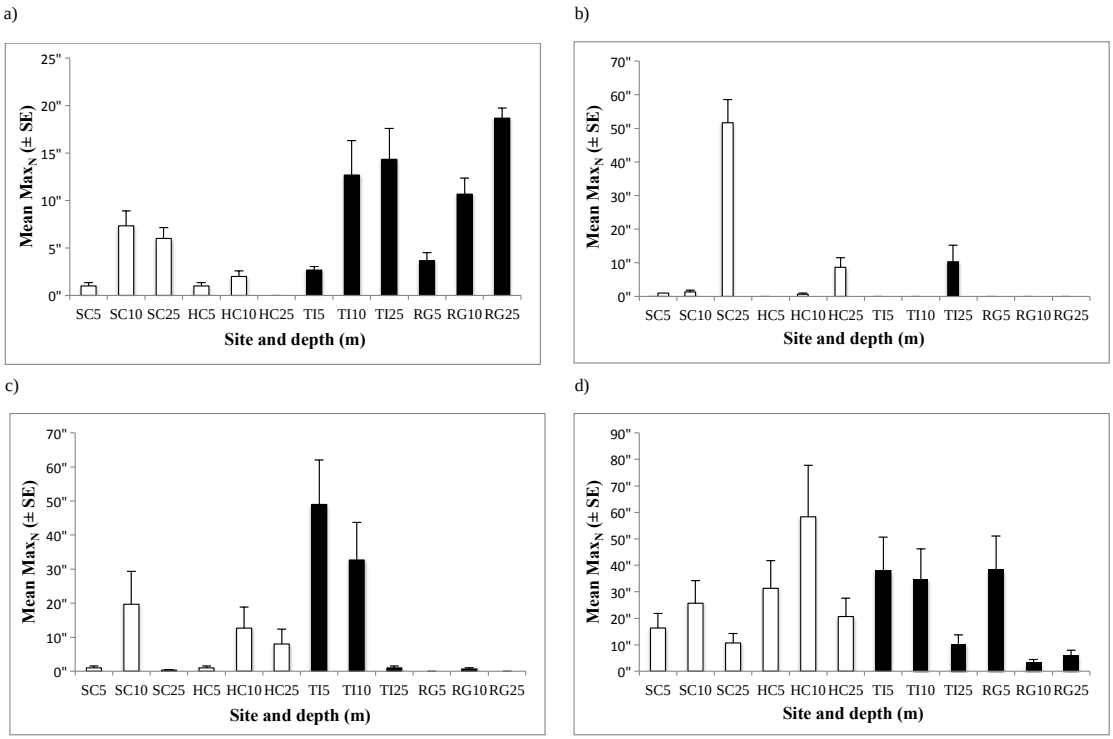


Figure 6. Histograms of the distribution of the mean maximum number of individuals observed at once in the camera field of view (Max_N) at the four sites; South Cove (SC), Hangar Cove (HC), Rose Garden (RG) and Trolval Island (TI) at three depths; 5, 10 and 25 m, for the Antarctic scavengers; a) *Odontaster validus*, b) *Ophionotus victoriae*, c) *Parbolasia corrugatus*, d) *Sterechinus neumayeri*.

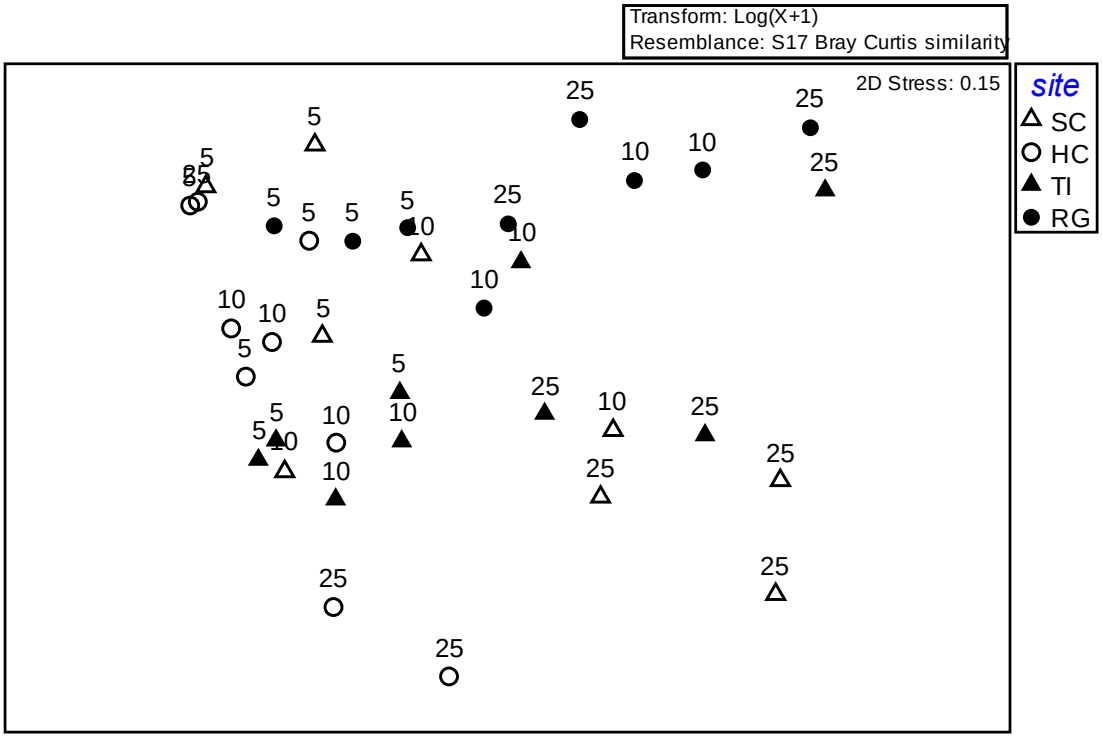


Figure 7. Non-metric multi-dimensional scaling plot of site similarities based on the Bray-Curtis similarity matrix applied to scavenger relative abundance as measured by the maximum number of scavengers at the baited underwater camera in one image (Max_N).

Site	GPS Position	Date	Start Time	Duration (minutes)	Depth (m)	Mean Current Speed (m/s ± SE)	Mean Current Direction (degrees ± SE)
Hanger Cove	67 33.84S, 68 07.50W	29/12/2011	09:37	90	10	0.066 ± 0.006	214.618 ± 5.500
South Cove	67 34.17S, 68 07.84W	31/12/2011	09:52	90	10	0.072 ± 0.005	203.148 ± 6.507
Hanger Cove	67 33.84S, 68 07.50W	02/01/2012	09:49	90	5	0.022 ± 0.002	115.777 ± 6.778
Rose Garden	67 36.76S, 68 12.71W	02/01/2012	15:09	90	25	0.663 ± 0.040	224.824 ± 5.339
Trolval Island	67 35.70S, 68 07.50W	03/01/2012	14:49	90	5	0.021 ± 0.001	170.673 ± 10.840
Rose Garden	67 36.76S, 68 12.71W	04/01/2012	09:36	90	5	0.025 ± 0.002	171.481 ± 8.427
Trolval Island	67 35.70S, 68 07.50W	05/01/2012	10:28	90	10	0.022 ± 0.001	90.927 ± 5.915
Hanger Cove	67 35.70S, 68 07.50W	05/01/2012	15:17	90	10	0.032 ± 0.002	117.481 ± 10.469
Rose Garden	67 36.76S, 68 12.71W	07/01/2012	09:51	90	10	0.050 ± 0.002	140.347 ± 3.777
Hanger Cove	67 33.84S, 68 07.50W	09/01/2012	10:42	90	25	0.094 ± 0.006	185.349 ± 9.276
South Cove	67 34.17S, 68 07.84W	11/01/2012	11:10	90	5	0.036 ± 0.001	96.739 ± 8.287
South Cove	67 34.17S, 68 07.84W	13/01/2012	10:17	90	25	0.051 ± 0.002	170.152 ± 8.926
Trolval Island	67 35.70S, 68 07.50W	14/01/2012	09:36	90	25	0.021 ± 0.001	177.866 ± 5.475
Trolval Island	67 35.68S, 68 13.02W	16/01/2012	09:32	90	10	1.240 ± 0.042	244.971 ± 11.282
Rose Garden	67 36.77S, 68 12.88W	18/01/2012	10:21	90	5	0.027 ± 0.002	164.972 ± 5.422
Hanger Cove	67 33.85S, 68 07.46W	19/01/2012	09:48	90	5	0.021 ± 0.002	205.653 ± 10.886
South Cove	67 34.17S, 68 07.94W	19/01/2012	15:05	90	5	0.026 ± 0.001	272.874 ± 10.882
South Cove	67 34.17S, 68 07.94W	20/01/2012	09:25	90	10	0.030 ± 0.001	108.893 ± 5.274
Rose Garden	67 36.77S, 68 12.88W	23/01/2012	10:31	90	10	0.031 ± 0.002	211.025 ± 11.681
Trolval Island	67 35.68S, 68 13.02W	24/01/2012	14:41	90	25	0.029 ± 0.001	130.158 ± 10.233
Trolval Island	67 35.68S, 68 12.79W	25/01/2012	09:51	90	10	1.398 ± 0.027	80.473 ± 8.581
Rose Garden	67 36.77S, 68 12.88W	25/01/2012	15:22	90	25	0.027 ± 0.002	181.695 ± 8.810
Hanger Cove	67 33.86S, 68 07.50W	27/01/2012	09:45	90	10	0.038 ± 0.002	249.168 ± 13.292
Hanger Cove	67 33.85S, 68 07.46W	28/01/2012	09:57	90	25	0.025 ± 0.002	110.659 ± 11.874
Trolval Island	67 35.68S, 68 12.79W	30/01/2012	12:22	90	25	0.034 ± 0.002	226.416 ± 5.416
Rose Garden	67 36.68S, 68 12.38W	31/01/2012	10:16	90	10	0.032 ± 0.001	208.64 ± 3.482
South Cove	67 34.16S, 68 08.00W	01/02/2012	11:12	90	5	0.037 ± 0.001	126.592 ± 4.063
South Cove	67 34.16S, 68 08.00W	03/02/2012	10:25	90	10	0.048 ± 0.002	148.733 ±1 0.561
Trolval Island	67 35.68S, 68 13.02W	03/02/2012	15:33	90	5	0.042 ± 0.001	118.189 ± 2.364
Rose Garden	67 36.68S, 68 12.38W	06/02/2012	10:56	90	25	0.034 ± 0.002	131.773 ± 6.562
South Cove	67 34.17S, 68 07.94W	07/02/2012	14:58	90	25	0.057 ± 0.002	235.8 ± 4.249
Rose Garden	67 36.68S, 68 12.38W	08/02/2012	09:22	90	5	0.042 ± 0.002	96.089 ± 9.038
South Cove	67 34.16S, 68 08.00W	09/02/2012	11:29	90	25	0.044 ± 0.001	246.334 ± 7.153
Hanger Cove	67 33.86S, 68 07.50W	21/02/2012	11:53	90	25	0.034 ± 0.001	155.842 ± 2.979
Hanger Cove	67 33.86S, 68 07.50W	22/02/2012	16:40	90	5	0.034 ± 0.002	235.401 ± 4.805
Trolval Island	67 35.68S, 68 13.02W	25/02/2012	09:51	90	5	0.044 ± 0.001	156.786 ± 3.878

Table 1. Details of baited camera deployments at Ryder Bay, Western Antarctic Peninsula.

Class	Species	Site	Depth (m)
Actinopterygii	*Notothenia coriiceps*	TI	25
	Harpagifer antarcticus	HC, SC, TI	10
Anopla	*Parborlasia corrugatus*	All	All
Asteroidea	*Odontaster validus*	All	All
	Cryptasterias turqueti	RG, SC, TI	10, 25
	Perknaster aurorae	RG	25
	Diplasterias brucei	SC	25
	Porania antarctica glabra	SC	25
Echinoidea	*Sterechinus neumayeri*	All	All
Malacostraca	*Glyptonotus antarcticus*	RG	25
Ophiuroidea	*Ophionotus victoriae*	All	10, 25
Polychaeta	*Flabelligera mundata*	SC	25

Table 2. Complete list of scavenger taxa observed in baited underwater camera deployment at Hangar Cove (HC), Rose Garden (RG), South Cove (SC) and Trolval Island (TI) at 5, 10 and 25 m.

Dependent Variable	Model	Independent Variable	Z-value	P-value
Species Richness	Richness ~ Depth	Depth	2.128	0.056
Shannon Wiener	H' ~ Depth	Depth	2.478	0.031
Total Max_N	Max_N ~ Depth + Impact Condition + Site	Depth	3.195	0.001
	+ Depth * Site + Depth * Impact Condition + Site * Impact Condition	Impact Condition	3.535	0.0004
		Site	3.018	0.003
		Depth * Site	-3.428	0.001
		Depth * Impact Condition	-3.337	0.0008
		Site * Impact Condition	-2.960	0.003
Odontaster validus Max_N	Max_N ~ Depth + Site + Site * Impact Condition	Depth	4.074	<0.0001
		Site	-2.498	0.013
		Site * Impact Condition	-2.444	0.015
Ophionotus victoriae Max_N	Max_N ~ Depth	Depth	-0.001	<0.0001
Parborlasia corrugatus Max_N	Max_N ~ Depth + Impact Condition + Site	Depth	2.024	0.043
	+ Depth * Impact Condition + Site * Impact Condition	Impact Condition	3.420	0.001
		Site	1.980	0.048
		Depth * Impact Condition	-2.280	0.023
		Site * Impact Condition	-2.672	0.008
Sterechinus neumayeri Max_N	Max_N ~ Depth + Impact Condition + Site	Depth	0.009	0.002
		Impact Condition	-3.138	0.039
		Site	2.516	0.012
		Site * Impact Condition	-2.583	0.001

Table 3. Results of GLM models to examine the relationships between scavenger species richness, the Shannon wiener diversity index and the total maximum number of individuals observed at once in the camera field of view (Max_N), the Max_N of the species (*Odontaster validus, Ophionotus victoriae*, *Parbolasia corrugatus, Sterechinus neumayeri*) and depth, scouring impact factor and site.

Source	d.f.	Max_N		
		MS	Pseudo-*F*	Perm(*P*)
Depth	2	6025.60	8.49	0.001
Scouring Condition	1	6507	2.24	0.35
Site (Scouring Condition)	2	2903.20	4.09	0.005
Depth x Scouring Condition	2	1767	2.49	0.022
Depth x Site (Scouring Condition)	4	1037.4	1.58	0.144

Table 4. PERMANOVA results for the relative abundance, as measured by the total maximum number of individuals observed at once in the camera field of view (Max_N), of scavenger assemblages sampled by BUC deployments at different depths, scouring impact factors and site.

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